ON THE RELATION BETWEEN WATER TRANSPORT AND FOOD REQUIREMENTS IN SOME MARINE FILTER FEEDING INVERTEBRATES

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Filter feeding invertebrates in the sea, *e.g.,* sponges, ascidians, most lamellibranchs, several gastropods and crustaceans, etc., obtain their food from the finely dispersed organic matter which is present in the water. A minor fraction of this organic matter is particulate and can be removed from the water by means of suitable filters, whereas a major fraction is "dissolved." It is not finally settled whether filter feeders obtain their food from the particulate fraction only, or whether they are also able to utilize the so-called dissolved organic matter in the sea. The view that filtering animals utilize the dissolved substances is mainly supported by calculations showing that particulate organic matter is not present in sufficient amounts to cover the energy requirements of the filter feeders. The calculations are based on measurements or estimates of rate of water transport, oxygen consumption and growth of the animals in question. The calculations are, however, somewhat uncertain because in no instance have water transport and metabolic rate been determined in the same specimen. It was therefore decided to measure filtration rate and oxygen consumption in the same individuals of some filter feeders and to repeat the calculations mentioned above.

TECHNIQUE

The species used were the oyster, *Ostrea virginica,* and the ascidians *Ciona intestinalis* and *Molgula manhattensis.* Experiments were performed on one oyster at a time or on 5 Ciona or about 15 Molgula. The oysters were kindly supplied by Dr. Paul S. Galtsoff, Shellfish Laboratory, U. S. Fish and Wildlife Service, Woods Hole. They had been living in the tanks of the laboratory for about a month. Ciona and Molgula were used in the experiments after they had been adapted to the laboratory conditions for a day. Filtration rates were determined as previously described (Jørgensen, 1949a) by measuring the rates at which graphite particles ("Aquadag A") were removed by the animals. Graphite concentrations were measured by means of a Klett-Summerson photoelectric colorimeter. Control experiments showed that the particles used were retained almost completely in the filtering organs (Jørgensen and Goldberg, unpublished data). Oxygen was determined by the Winkler method.

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RESULTS

The results of the experiments are shown in Figures 1–4. The points in the graphs represent single determinations of filtration rate or oxygen consumption in liters of water or milliliters of oxygen per hour. It is seen that the rate of water transport was of the same order throughout the period of observation which lasted three to four days. In Ostrea and Molgula, the water transport was approximately
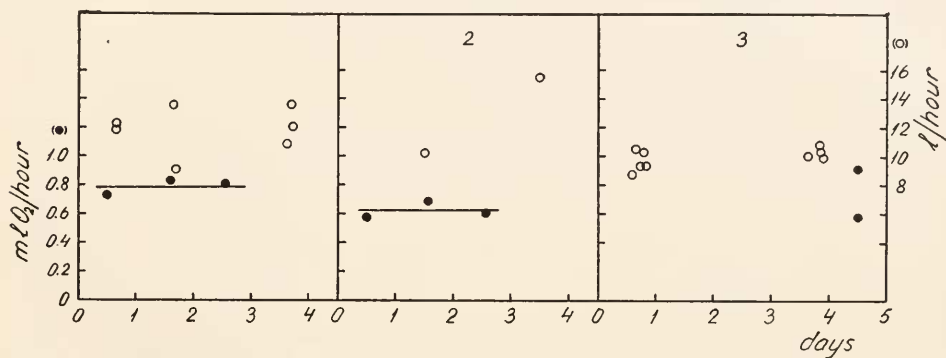

FIGURE 1. *Ostrea virginica.* ● Oxygen uptake in ml. per hour. ○ Filtration rate in liters per hour. Experiments on three individuals.
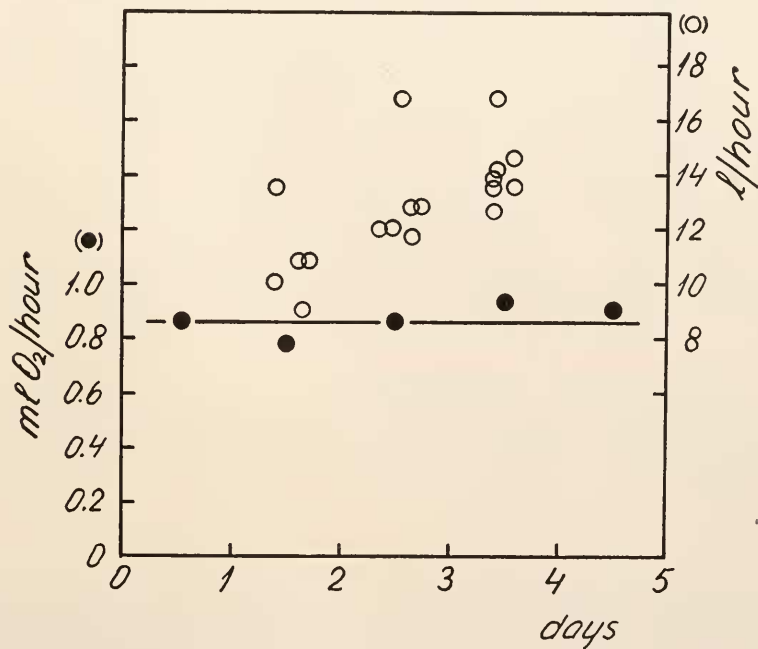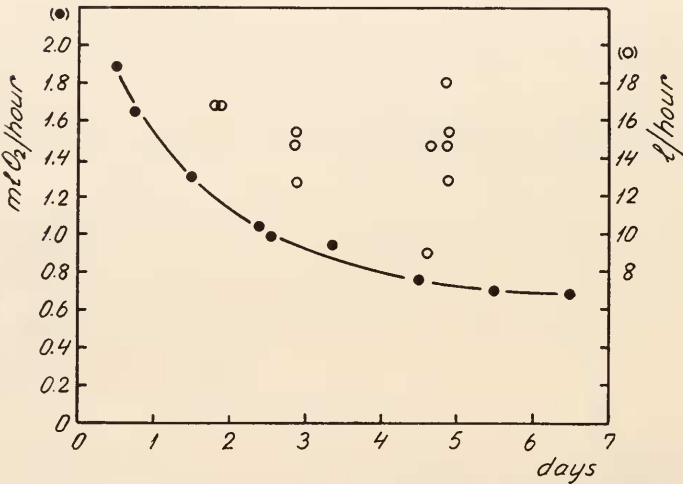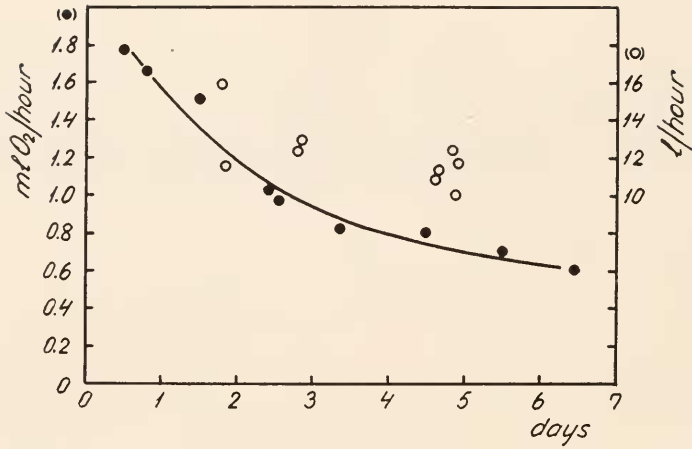

FIGURE 2. *Ciona intestinalis;* 5 specimens. ● Oxygen uptake in ml. per hour. ○ Filtration rate in liters per hour.

Figures 3 and 4. *Molgula manhattensis*. About 15 specimens. ● Oxygen uptake in ml. per hour. ○ Filtration rate in liters per hour.

constant from day to day. In Ciona, filtration rates were lower the first day than the two following days, probably because the animals became better adapted to the experimental conditions with time. The oxygen uptake was constant in the oyster and Ciona, but decreased with time in Molgula.

DISCUSSION

From Figures 1 and 2 it is seen that the oyster and Ciona pumped about 10 to 20 liters of water through their filtering organs for each ml. of oxygen uptake. In Molgula the ratio between water transport and metabolic rate is not well defined because oxygen was consumed at decreasing rates throughout the experiments. There is reason to believe that at least two factors are responsible for the decrease in

oxygen uptake. On arrival in the laboratory hydroids, bryozoans, algae, etc. growing on the mantle of the animals were removed. This procedure, which also involved separation of adhering animals, may have caused an increase in metabolic rate so that the rates of oxygen uptake have perhaps been abnormally high during the first days of the experiments. Mytilus when detached from their support by tearing of the byssus threads were also found to respond by strongly increasing their oxygen consumption. Thus, the steady decrease in metabolic rate of Molgula may just indicate a slow return towards values of oxygen uptake characteristic of undisturbed animals. However, poor food conditions may also be partly responsible for the continued decrease in oxygen consumption as pointed out below. Probably, therefore, normal metabolic rates are to be found somewhere in between the rates which were measured at the beginning and at the end of the experiments. If the measurements made on the third day of the experiments are used as "normal" values we find also in Molgula that about 10 to 20 liters of water are filtered for each ml. of oxygen uptake. Filtration rates of the same order were also measured in *Mytilus edulis, Pecten latiauritus* and *Ciona intestinalis* from coastal waters off Southern California (unpublished data).

The literature contains data on feeding rate and oxygen uptake in other filter feeders. Even when these data are not obtained from the same individuals and under identical experimental conditions, they are consistent with the results of the present study.

In the copepods *Calanus finmarchicus* and *Centropages hamatus,* feeding rate and oxygen uptake have been measured by Gauld (1951) and Raymont and Gauld (1951), respectively. From their figures, filtration rates of about 8 to 10 liters of water per ml. of oxygen uptake can be calculated.

Jørgensen (1949b) found that the silicious sponge *Halichondria panicea* filtered 65 ml. of water per hour and per mg. nitrogen (18–19° C.). Pütter (1914) measured the oxygen uptake in another silicious sponge, *Suberites massa,* to be 0.34 ml. per hour and per gram dry organic matter (22° C.). Assuming a content of 8 per cent nitrogen, this means 4.2 ml. O_2/hour/mg. nitrogen. Thus, if these values for water filtration and oxygen uptake are generally valid in silicious sponges, 15 liters of water are filtered for each ml. of oxygen uptake. The calcareous sponges *Grantia compressa* and *Sycon coronatum* showed pumping rates of about 140–200 ml./hour/mg. nitrogen (Jørgensen, 1949b). Probably, therefore, their filtration rate relative to metabolism is of the same order as that of the silicious sponges, perhaps even higher.

In phylogenetically unrelated filter feeders which use different filtering mechanisms, the rates of filtering and the metabolic rates have been adjusted to about the same ratio. Presumably the feeding rate, not the filtration rate as such, is primarily adjusted relative to the metabolic rate (and relative to the rate of growth). A constant ratio between rates of filtration and of oxygen uptake in different filter feeders therefore suggests that the concentration of available food in the sea where adaptation took place was about the same for all the filter feeders mentioned above. This conclusion of course rests on the assumption that the rate of filtration of the animals is the same in their natural environment as under the conditions of experiment. However, there is some reason to believe that this assumption holds. Food conditions must be better in the sea than in the running tap water of the laboratory

where much food is removed by other organisms growing in storage tanks and water pipes. The decrease in oxygen uptake observed in the course of an experiment in Molgula (Fig. 3 and 4) and in Mytilus and Pecten (unpublished) is probably partly due to starvation. However, filtration rates were not influenced by the reduction in food concentration. Filtration rates of lamellibranchs and ascidians are also independent of increased concentrations of food and other particles as long as the concentrations are not too high (Loosanoff and Engle, 1947, and others). Thus, if filtration rate can adjust to different food levels, this process must be slow. Hence, when measured with a suitable technique [2] the pumping rate and the oxygen uptake in undamaged animals which have been adapted to the laboratory conditions are therefore probably representative of the corresponding rates prevailing in the sea.

"Available food." The organic matter in the sea is present as organisms such as phytoplankton, bacteria, Protozoa, etc., but also as dead material such as decaying plants and animals. The organic matter varies greatly in particle size; phytoplankton cells, for example, range from about one to several hundred micra. The decaying material (detritus), of course, has no well-defined particle size and there is no sharp distinction between particulate and dissolved organic matter. Such a distinction, however often made, must therefore be a rather arbitrary one. "Particulate" material usually means material retained by paper or membrane filters with pore diameters of about one micron, whereas "dissolved" and "colloidal" matter passes through such filters. In this paper particulate organic matter is assumed to have a particle size of about one micron or more. The composition and the physical properties, such as particle size, of "dissolved" or "colloidal" organic matter are practically unknown. The latter is an important fraction, generally amounting to several times the particulate fraction. Values of dissolved organic nitrogen from various parts and depths of the sea range from 0.1 to 0.26 mg. per liter (Krogh and Keys, 1934, and von Brand and Rakestraw, 1941). Dissolved organic carbon is present in an amount of about 2.36 mg./liter. Assuming a mixture of carbohydrate and protein this would mean that about 1.5 mg. protein and 3.9 mg. carbohydrate are dissolved per liter of sea water (Krogh, 1934). The amount of particulate organic matter, living or dead, varies more than does that of dissolved matter. Some figures representative of coastal waters are given in Table I. Values from open sea and from great depths are smaller. However, the figures from coastal waters are of special interest to us because all determinations of filtration rates in filter feeders are gained in such areas.

It has often been discussed whether sufficient particulate organic matter is present in the water to cover the food requirements of filter feeders or whether dissolved or colloidal matter has to be taken into consideration as an additional resource. This discussion will not be reviewed here in detail. It should only be pointed out that the different approaches to the problem have led to contradictory results. One approach has been to estimate how much water should be filtered free of particulate food in order to meet the energy requirements of the animal in

[2] By "suitable technique" is meant a technique which does not significantly interfere with the normal filtering activity of the animal. Generally, even slight handling or disturbances of a filter feeder will reduce filtration rate. The values of water transport given in the present paper, as in other papers, are therefore more likely to be too low than too high.

question. Pütter (1909, 1914, 1925) made extensive studies on a variety of marine animals and concluded that the necessary filtration rates were beyond reasonable values. Fox and Coe (1943) made similar calculations for *Mytilus californianus*. They state that the quantity of micro-organisms present in the water does not provide enough nutriment for growth and metabolism of the mussel. They therefore conclude that about 5 mg. of organic matter, found by Krogh to be in solution in sea water, must be accessible to the mussels as food. On the other hand, direct attempts to demonstrate the importance as food of dissolved organic substances, either added or naturally occurring in the water, turned out negative (Krogh, 1931; Bond, 1933; and others).

It is of interest to repeat the calculations on the basis of our present knowledge of metabolic, growth and filtration rates, and to relate the results with the quantity of particulate organic matter which can be assumed to be present in the water.

TABLE I

Locality	Phytoplankton mg. organic matter per liter		Author	Remarks
	Range	Average		
English Channel	0.04–0.2 0.01–0.23	0.06	Harvey, 1950 Atkins and Parke, 1951	Annual variation Annual variation
Baltic Sea	0.35		Krey, 1939	March
Long Island Sound	0.17–2.1 0.6 –2.8	0.59	Riley, 1941 Riley, Stommel and Bumpus, 1949	June–October June–September
Block Island Sound		0.38	Riley, personal communication	
Coastal water south of Cape Cod	0.14–0.63		Riley and Gorgy, 1948	July–September
Coastal water off La Jolla	0 –0.22	0.09	Graham, 1943	Annual variation

The calculations are based on a filtration rate of 15 liters for each ml. of oxygen uptake. One ml. of oxygen is required to combust about 0.8 mg. organic matter of mixed food. Fifteen liters of water should therefore contain at least 0.8 mg. organic matter which can be retained and utilized by the animals, or about 0.05 mg./liter. Obviously, organic matter which is used for growth must also be taken into consideration. The efficiency with which absorbed nutrients are utilized for growth varies with the age of the animals. In filter feeders such as lamellibranchs, gastropod veligers or copepods, up to about $\frac{2}{3}$ of the energy absorbed can be used for growth (Harvey, 1950, and Jørgensen, 1952). Therefore, the actual food requirements for growth and respiration of the animals investigated probably does not exceed about 0.15 mg. utilizable organic matter per liter of water. The average figures for

phytoplankton (Table I) range from 0.06 mg. to 0.59 mg./liter, the lowest figure being found in the English Channel. Here, total organic particulate matter is, however, 1.6–1.8 mg./liter (Armstrong and Atkins, 1951). The values from La Jolla are perhaps too low because, in some instances, very little or no chlorophyll was measured despite rather high counts of chlorophyll-containing algae cells in the water. Thus at least during part of the year, particulate organic matter, phytoplankton and detritus, in the coastal waters is in excess of the amount needed for maintenance and growth of a number of filter feeders. The shortcoming of previous calculations is due mainly to an under-estimation of filtration rates, but also of the amount of particulate food in the sea.

It remains to be demonstrated that the filtering organs of the filter feeders are in fact able to retain what is generally measured as particulate organic matter in the sea, *i.e.,* material with a minimum particle size of about one micron. The efficiency of the filtering organs has been investigated in rather few species only. It was found that *Ciona intestinalis* almost completely retains one-micron particles. The same is probably true of other tunicates as well as sponges. In the lamellibranchs Mytilus, Ostrea and Pecten, the minimum particle size effectively retained varied from about one to a few micra (Jørgensen, 1949a, and Jørgensen and Goldberg, unpublished data). This probably also holds for many copepods (Ussing, 1938). Thus, most of the particulate organic matter in the sea is available to at least a considerable number of filter feeders.

Adjustment of food requirements to rate of food uptake. As mentioned above, changes in the concentration of food particles were not accompanied by changes in filtration rate.[3] The feeding rates therefore decrease with decreasing quantities of food in the water. Perhaps the reduction in metabolic rate to be observed in the course of the experiments with Molgula and other filter feeders can be interpreted as an adaptation to poor feeding conditions. Pütter (1914) observed a similar decrease in oxygen uptake in the sponge Suberites, and it is worth mentioning that v. Brand *et al.* (1948) found striking reductions (up to 80 per cent) in metabolic rates during starvation in a number of pulmonate gastropods.

However, more information is needed before we can obtain a clear picture of the interdependence between rate of filtration, metabolism, growth of different filter feeders and the concentration of food particles in the surrounding water.

Summary

The oyster, *Ostrea virginica,* and the ascidians *Ciona intestinalis* and *Molgula manhattensis* filter about 10 to 20 liters of water for each milliliter of oxygen consumed. It has been demonstrated that this filtration rate is probably great enough to provide the animals with sufficient amounts of particulate food for maintenance and growth.

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[3] It is unknown whether a slow adaptation of filtration rate to different concentrations of food particles can take place.

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